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A Population Viability Analysis for the Puritan Tiger Beetle in the Chesapeake Bay Region

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Introduction

This report presents a population viability analysis (PVA) for Puritan tiger beetle (*Cicindela puritana*) populations in the Chesapeake Bay region. The beetle is currently listed under the Endangered Species Act (ESA), and a recovery plan has been prepared (USFWS 1993). For the purposes of the recovery effort, the sub-populations are grouped into two distinct geographic areas, both in Maryland (Calvert County and the Sassafras River; Figure 1). The recovery plan calls for protection of at least six, large (>500 adults) sub-populations in each area. However, there is still uncertainty about how best to protect beetle habitat in order to promote recovery. In particular, because the beetle exists as a series of distinct sub-populations within each area, better information is needed regarding how many and which particular sub-populations merit strongest protection. The goal of this PVA analysis is to provide a more reliable basis for deciding on numbers and locations of sites to protect in each area.

Methods

Study Area

The beetles currently exist as 18 sub-populations distributed along the eastern and western shores of Maryland, with an individual population consisting of a few to >1,500 beetles (Figure 1; Table 1). The PVA was designed to examine population viability for each geographic area.

Table 1. Information on 18 Puritan tiger beetle sub-populations located in the Chesapeake Bay region. Protected status refers to the current regulatory status of each location (P = protected as a state, federal or private preserve, NP = not protected). UTM = Universal Transverse Mercator location, WGS84, Zone 18. Only populations with K>0 were included in the metapopulation model. Starting population size was the population size used in Year 1 of the metapopulation model. NRMA= Natural Resource Management Area.

Site	UTM Northing	UTM Easting	Area	Length (m)	Protected status	Carrying Capacity	Starting Population
Randle	4281769	366773	Calvert	889	NP	142	142
Camp Roosevelt	4277935	367588	Calvert	1283	NP	0	0
Bayside Forest	4270906	367892	Calvert	1535	NP	123	123
Scientists Cliffs	4263883	368427	Calvert	3853	NP	458	458
Parker Marsh South	4265725	367864	Calvert	812	P	618	618
W. Shore/Calvert Beach	4259574	370512	Calvert	627	NP	1656	1656
Calvert Cliffs State Park	4252110	376774	Calvert	1335	NP	1483	1483
Calvert Cliffs Nuclear Plant	4254195	375090	Calvert	1471	NP	337	337
Little Cove Point	4246787	378123	Calvert	2894	NP	819	819
Cliffs of Calvert	4244680	377291	Calvert	1512	NP	189	189
Grove Point	4361196	410927	Sassafras	1995	NP	452	452
Ordinary Point	4359580	414767	Sassafras	885	NP	86	86
North Still Pond	4356157	402311	Sassafras	998	NP	207	207
West Betterton	4358587	406269	Sassafras	2758	NP	148	148
East Betterton	4358316	409848	Sassafras	540	NP	27	27
East Lloyd Creek	4357462	412008	Sassafras	202	NP	88	88
Sassafras NRMA	4357976	413245	Sassafras	1656	P	19	19
East Turner	4357565	415860	Sassafras	237	NP	15	15

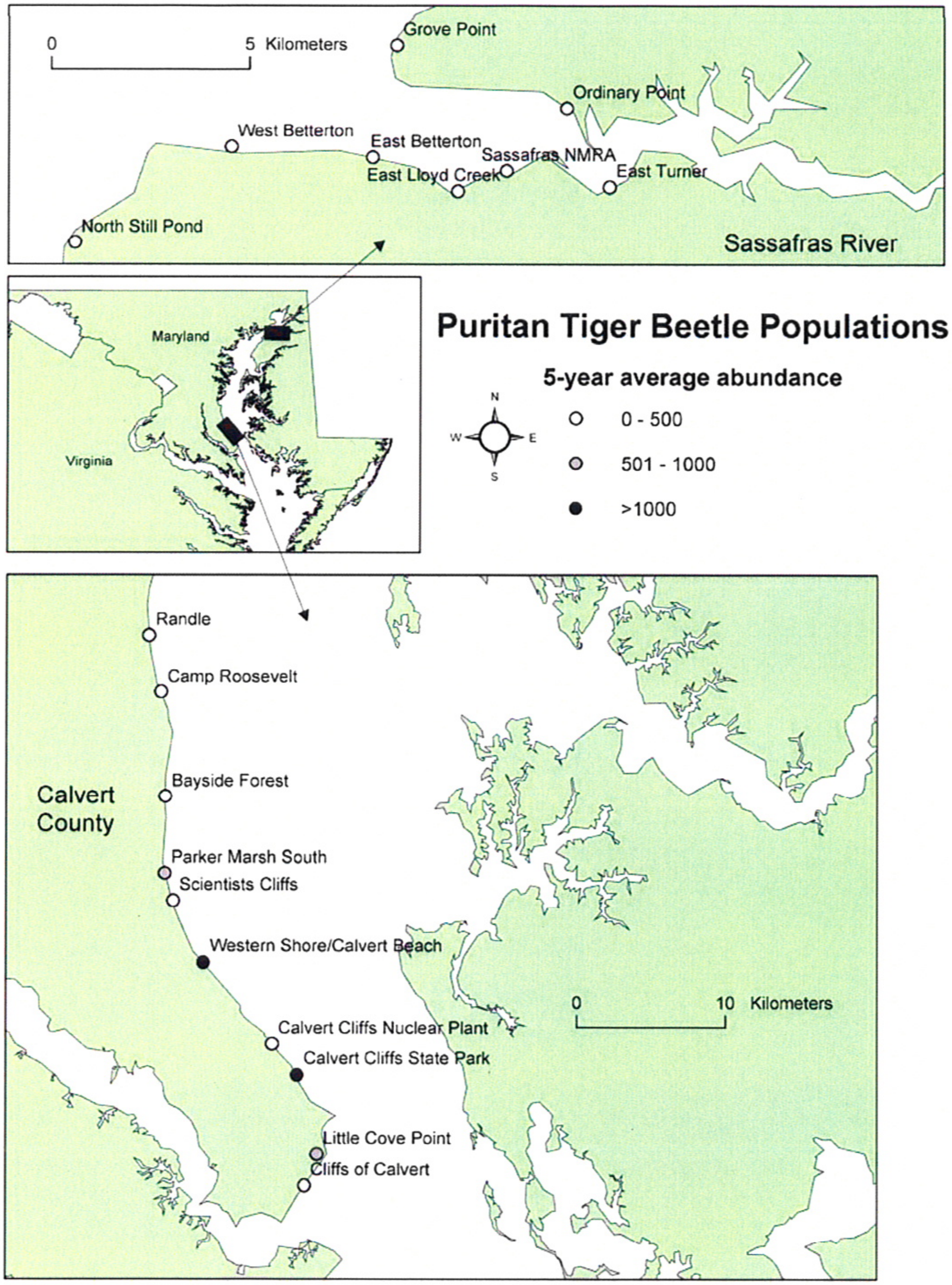

Figure 1. Puritan tiger beetle populations located near the Sassafras River (upper panel) and in Calvert County, Maryland (lower panel).

General Modeling Approach

The individual tiger beetle sub-populations within each geographic area were assumed to operate together as a metapopulation. To conduct the PVA, a metapopulation model was developed that accounted for population growth within sub-populations, dispersal between sub-populations, and the degree to which inter-annual variations in population growth rates were correlated. The model was used to predict the probability that the beetle population would decline to zero, or other specified thresholds, within the next 100 cohorts under a series of management strategies that involved protection of different sets of sub-populations. The goal was to determine which particular set of sub-populations, if protected, would give an acceptably-low risk of extinction.

It must be cautioned that the main purpose of the analysis was to compare management strategies, not to estimate extinction probability per se. Accurate estimates of extinction probability require reliable estimates for each of the parameters in the metapopulation model, including population growth rates, interannual variation in growth rates, carrying capacities, dispersal rates, and correlation among sub-populations. Although estimates based on our current knowledge of the species were generated for each of these parameters, they are not dependable enough to provide trustworthy estimates of true extinction probability. However, the estimates are reliable enough to compare the effectiveness of different management strategies. The goal was to determine which strategy reduced extinction risk the most, even if the exact extinction risk could not be quantified with certainty. In order to evaluate the influence of alternative parameter estimates on the relative rankings of the different management strategies, a sensitivity analysis was conduced. This analysis (described later) examined the effects on predicted extinction risk of changing several of the model parameters.

Estimating Model Parameters

Before the model could be used to examine different management strategies, parameter values had to be developed. Three items were of particular importance. First, a population growth model had to be developed in order to predict annual increases or decreases in abundance within each sub-population. Next, the correlation among sub-populations in their population growth rate had to be estimated. Finally, the dispersal rate among sub-populations had to be quantified. Each of these issues was examined using empirical data collected during previous monitoring and other studies funded by the U.S. Fish and Wildlife Service.

Modeling population growth within sub-populations

Population viability analyses are usually based on age- or stage-based population models requiring input data such as transition and survival probabilities between lifestages, and stage-specific fecundity rates. Because this information was not available for the Puritan tiger beetle, an alternative approach was developed based on empirical observations of sub-population dynamics in sub-populations monitored annually between 1988 and 2004 (Figure 2). The basic concept was to model future dynamics for all sub-populations based on statistics obtained from six sub-populations monitored intensively between 1988-2004. Although some monitoring occurred at other sites, we feel data from these six sites are the most reliable for quantifying population growth because these sites were consistently monitored since 1988. Where necessary, expert opinion of the second author was used to supplement available information.

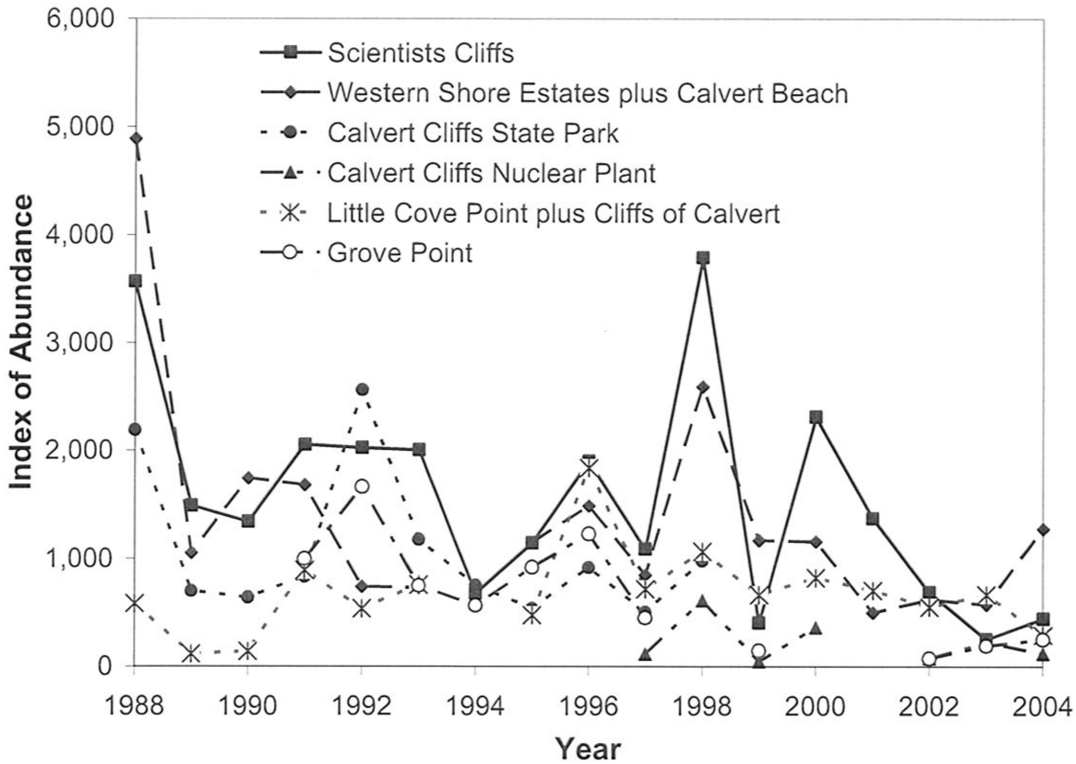

Figure 2. Index counts for adult tiger beetles in six sub populations, 1988-2004. Index counts were made by one observer moving along the entire length of beach habitat and counting all observed beetles during peak abundance and optimum conditions.

In selecting a population model, we first analyzed the observed dynamics to determine if each population exhibited density dependence. Because the beetles have a two-year lifecycle with distinct cohorts, density dependence could occur on either a one or two year interval. A two-year interval makes intuitive sense because it means that the density dependence is based on interactions between the same life stage (e.g., number of adults in one year affects number of adults two-years later). If density dependent effects influenced population dynamics on a two-year interval, the slope of a regression of population abundance in year t (N_t, log-transformed) on the rate of growth between year t and year $t+2$ ($N_{t+2}/N_t = \lambda$, log-transformed) should be negative. The same analysis can be done on a one-year interval, except that N_{t+1} replaces N_{t+2}. Results for both analyses were similar, so only those from the two-year interval will be presented for brevity. Growth rates over two-year intervals will be referred to as "cohort growth rates".

There was strong evidence of density dependence (Figure 3; by linear regression; P <0.0001 for the analysis of all sites combined; when analyzed individually, five of the six sites showed evidence of density dependence (P<0.1), the exception being the Calvert Cliffs Nuclear Plant population (P=0.46)). Based on this, a logistic growth model was selected.

Maximum cohort growth rate (λ_{max}) for the logistic model was estimated based on the observed growth rates for the six sub-populations monitored between 1988-2004 (Table 2). Average cohort growth rate (N_{t+2}/N_t) varied from 0.685 at Calvert Cliffs Nuclear Plant to 1.53 at Little Cover Point/Cliffs of Calvert. A value of 1.3 was selected for all sub-populations included in the metapopulation model because the growth rate in the metapopulation model is meant to represent the maximum rate that the population can achieve under ideal circumstances.

Table 2. Cohort population growth rate (λ) of tiger beetle populations averaged over available cohorts for six sites.

Site	*n* Cohorts	Mean λ	Standard Deviation
Scientists Cliffs	15	1.092	0.9616
Western Shore Estates plus Calvert Beach	12	1.170	0.8762
Calvert Cliffs State Park	9	1.207	1.1236
Calvert Cliffs Nuclear Plant	4	0.685	0.5731
Little Cove Point plus Cliffs of Calvert	13	1.531	1.9770
Grove Point	7	1.224	1.1078
Average		1.151	1.1032

One of the most important aspects in PVA is to account for the effects of stochastic events on population growth rate. This is especially true for invertebrate populations wherein temporal variation in abundance is probably due more to stochastic events in the environment rather than density dependent effects. Environmental stochasticity was incorporated into the model by

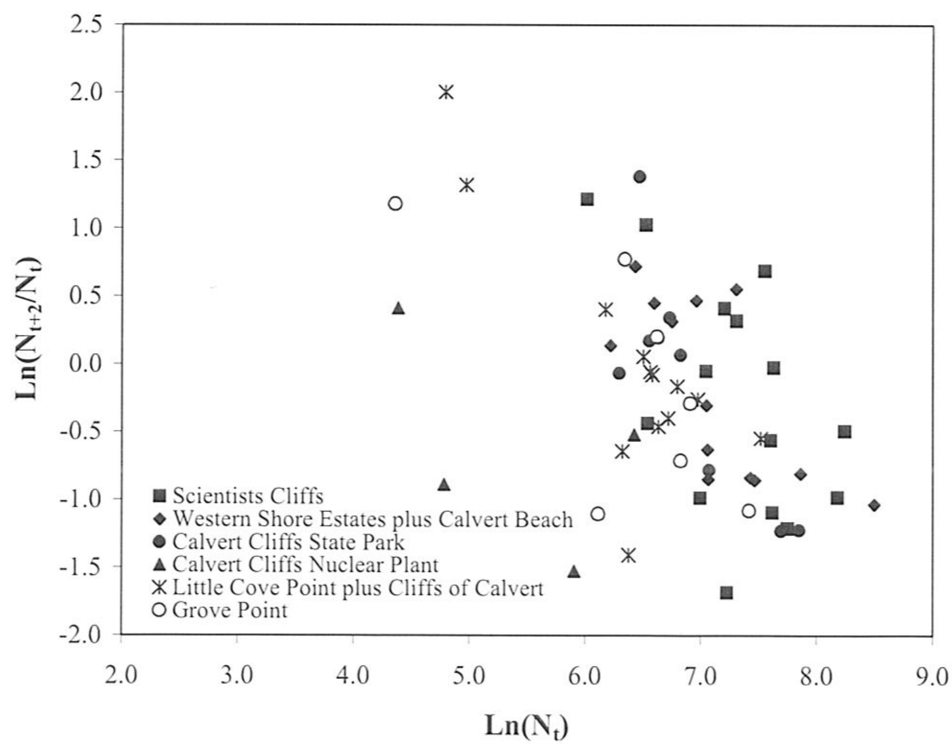

Figure 3. Regression of population growth rate (λ = N_{t+2}/N_t) on population size (N_t) for six populations of Puritan tiger beetles during the years 1988-2004.

making annual population growth rate a random variable. That is, for each year in a simulation, the computer selected a random value for growth rate (λ_t where t indicates time) from a normal distribution with a user-specified mean (λ_{max}=1.3 as previously described) and standard deviation. If a higher value is selected for the standard deviation, then greater environmental stochasticity is incorporated in the metapopulation model because there is a greater potential for any given year to be extremely poor (λ_t is small) or extremely good (λ_t is large) in terms of population growth rate.

Appropriate values for the standard deviation of λ were based on the observed variation in sub-population growth rates between 1988-2004. The observed average standard deviation in sub-population growth rate was 1.10 (Table 2). However, this value may over-estimate actual variation because it includes variation in capture probability in different years. That is, because beetle abundance was estimated using index counts, some of the recorded variation in abundance was due to variation in the ability of the observers to detect and count beetles each year, and to variation in the number of beetles active at the time of the observations. Moreover, there is evidence of declining abundance over time (Figure 2), which would increase the estimated standard deviation of growth rate. Based on the opinion of the authors, a standard deviation of 0.55 (50% of the recorded value) was used in the metapopulation model.

The same mean and standard deviation of population growth rate was used for all sub-populations. However, each sub-population was given a unique carrying capacity (K) and starting population (Table 1). The K and starting values for each sub-population were based on index counts made periodically since 1988 in all sub-populations. In general, the average of index counts for the most recent five years available times 2 was taken as both K and starting population size. The index count averages were multiplied by 2 because various studies with several tiger beetle species showed that index counts underestimated true abundance by a factor of about 0.5. The sub-populations in Table 1 with a K of 0 were considered to be sinks; beetles were sometimes present there but were not considered a viable breeding population.

Modeling correlation in population growth among sub-populations

Although each sub-population is geographically distinct, it is reasonable to assume that they will often experience similar environmental conditions, such as good and bad weather. As such, there should be some degree of correlation in annual population growth rates, meaning that if one population experiences poor growth in a cohort, nearby ones probably will as well. This effect was incorporated into the metapopulation model by specifying the degree to which population growth rate was correlated among sub-populations.

To determine the degree to which tiger beetle population growth rates were correlated, data from the six sub-populations (Figure 2) were examined with a view towards quantifying the relationship between distance separating two populations and correlation between them in population growth rate (under the assumption that sub-populations that are close to one another will be more correlated than those that are distant). To quantify the relationship between correlation and distance, the correlation in population growth rate was calculated for each of the six sub-population pairs, and the distance between them measured. Based on these data (Table 3), a line was fit to the equation,

$$\rho_{ij} = e^{-D_{ij}/b} \quad \text{Equation 1}$$

where ρ_{ij} = the correlation coefficient between populations i and j,
D_{ij} = the distance (km) separating them, and,
b = a regression coefficient estimated from the data.

Table 3. Distance between six sub-populations and the correlation coefficient (p_{ij}) estimated by regressing λ_1 (cohort growth rate in sub-population 1) on λ_2 (cohort growth rate in sub-population 2) for the years 1988-2004. Negative correlations were assumed to be zero when analyzing the relationship between distance and correlation (see Figure 4).

Sub-population pair (sample size)	Distance (km)	p_{ij}, for cohort λ
Scientists Cliffs to Western Shore (n=12)	5.2	-0.14
Scientists Cliffs to Calvert Cliffs State Park (n=9)	14.8	0.39
Scientists Cliffs to Calvert Cliffs Nuclear Plant (n=4)	12.1	0.81
Scientists Cliffs to Little Cove Point (n=13)	20.4	0.22
Scientists Cliffs to Grove Point (n=7)	105.9	0.38
Western Shore to Calvert Cliffs State Park (n=6)	9.7	0.23
Western Shore to Calvert Cliffs Nuclear Plant (n=4)	7.1	0.51
Western Shore to Little Cove Point (n=12)	15.2	-0.18
Western Shore to Grove Point (n=5)	109.4	0.34
Calvert Cliffs State Park to Little Cove Point (n=7)	6.1	0.38
Calvert Cliffs State Park to Grove Point (n=5)	114.3	0.37
Calvert Cliffs Nuclear Plant to Little Cove Point (n=4)	8.5	-0.69
Little Cove Point to Grove Point (n=5)	119.8	-0.66

Based on the data in Table 3, the parameter b from Equation 1 was estimated to be 7.187, allowing us to predict the degree to which two sub-populations would be correlated based on the distance between them. Populations separated by >40 km were essentially uncorrelated, but correlation increased to 1.0 (perfect correlation) as the distance between sub-populations decreased to 0 km (Figure 4). Equation 1 was incorporated into the metapopulation model and used to predict the correlation in growth rate among all possible sub-population pairs. The net result was that populations close together (<40 km apart) tended to fluctuate up and down together, increasing the risk of extinction due to a single poor year affecting those populations together. Populations separated by >40 km fluctuated independently of one another, reducing extinction risk.

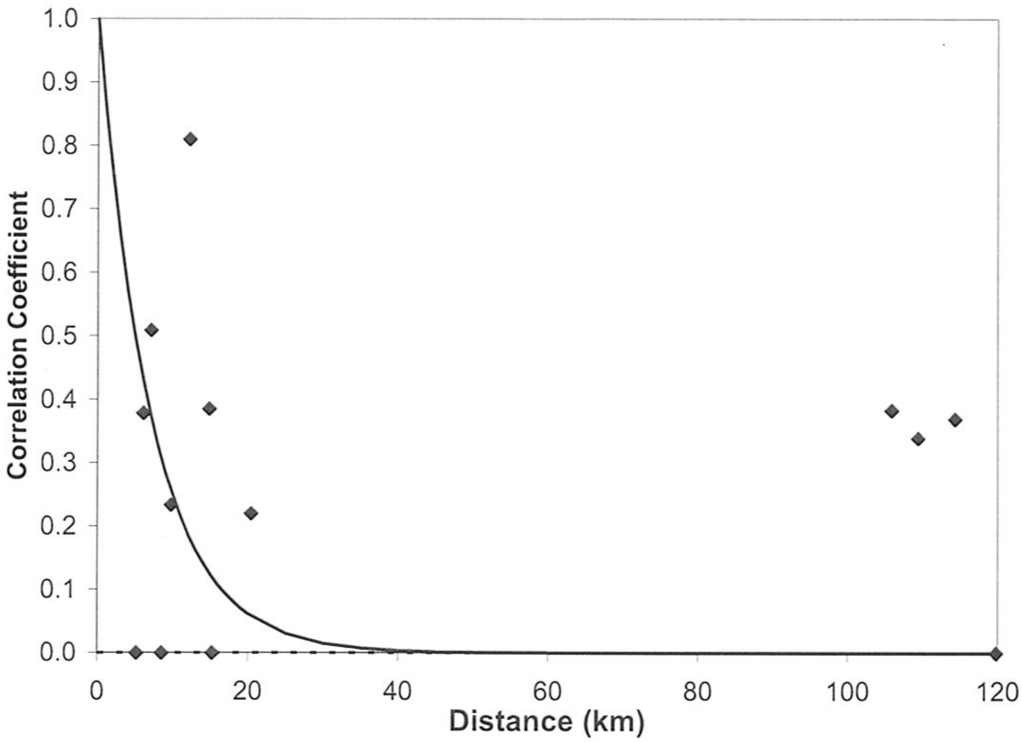

Figure 4. Relationship between distance separating two sub-populations and the correlation coefficient of growth rate estimated by regressing λ_1 (cohort growth rate in sub-population 1) on λ_2 (cohort growth rate in sub-population 2) for the years 1988-2004.

Modeling beetle dispersal among sub-populations

Metapopulations can sometimes persist longer than a single large population because extinct sub-populations (vacant habitat) can be recolonized by individuals from nearby extant ones. Thus, modeling dispersal is an important component in a metapopulation analysis.

An attempt was made to estimate beetle dispersal using a mark/recapture study conducted in 2003. A total of 651 beetles were marked at released at the Western Shores site between June 30 and July 7. Recaptures were attempted at Western Shores, Little Cove Point, Scientists Cliffs, Bayside Forest, Cliffs of Calvert, and Randle on July 15, 16, 20, 21, 25, 28, 29 and August 1, 2, 4, 5 and 11. However, a total of only 3 dispersers (one to Little Cove Point captured on July 15 and 2 to Scientists Cliffs captured on July 20th) were detected, a number too small to allow statistical analysis. Data provided by K. Omand from a population of *C. puritana* at sites on the Connecticut River in Connecticut were also examined, but because beetles were not individually-marked in that study, it was not possible to separate probability of dispersal (the parameter of interest) from capture probability and mortality rate (nuisance parameters). Thus, we had no reliable data upon which to estimate dispersal in *C. puritana*.

In lieu of data for *C. puritana*, we used mark/recapture data collected for the northeastern beach tiger beetle (*Cicindela dorsalis dorsalis*) We believe using *C. dorsalis* dispersal data is reasonable because the species occur in the same geographic area, use similar linear shoreline habitats, have a similar 2-year life-cycle and share other aspects of basic biology, and show similar variation in abundance over time. The sample sites were all in the Smith Point area of Northumberland County, VA Maryland and separated by 1.3 to 13.9 km. Five capture occasions took place between July 6 and August 23, 1994, involving a total of 10,131 beetles (Table 4). All captured beetles were marked to indicate location and date and released.

Table 4. Number of beetles marked during a 1994 mark/recapture study of *C. dorsalis dorsalis* to evaluate dispersal among five sites.

Site	Number Marked	Percent Recaptured at All Sites	Number Detected at Another Site
Smith Point North	3,470	42%	42
Smith Point South	1,981	47%	12
Taskmakers Creek	2,637	59%	7
Sandy Point	365	42%	14
Dameron Marsh	1,678	22%	4

It is reasonable to assume that beetles more easily disperse to nearby rather than distant sites. Thus, data from the dispersal study were examined with a view towards quantifying the relationship between distance separating two sub-populations and the probability that a beetle would disperse from one to the other. To quantify the relationship between dispersal and distance, dispersal rate between each sub-population pair (a total of 10 pairs) was estimated and the distance between them measured. Based on these data, a line was fit to the equation,

$$m_{ij} = e^{-D_{ij} / b} \qquad \text{Equation 2}$$

where m_{ij} = probability that a beetle will disperse between populations i and j, D_{ij} = the distance (km) separating them, and b = a regression coefficient that was estimated from the mark/recapture data.

Estimating dispersal based on mark/recapture data is difficult because the number of dispersers detected is a function of not only dispersal rate, but also capture probability and mortality. Thus, in order to obtain reliable estimates of dispersal rate, an open-population survival rate model was used. Such models are called multi-strata models (Brownie et al. 1993) because they simultaneously estimate capture, survival, and movement probabilities based on the model where:

p_i^s = probability of capture at time i, for an animal in location s at time i.

ϕ_i^{rs} = probability of being alive and in location s at time $i+1$ for an animal alive and in location r at time i.

The multi-strata survival and movement model included in Program MARK (written by Gary White, Colorado State University) was used to estimate movement probability between tiger beetle locations. A capture history was developed for each beetle included in the 1994 study based on the location/date marks each received. This capture history was input to Program MARK, and a series of models was developed by constraining various parameters to be equal to one another. For example, some models were constrained such that all capture probabilities were equal among locations, but varied by capture occasion. By developing a large number of models and testing them against one another, the most parsimonious model was identified. This model

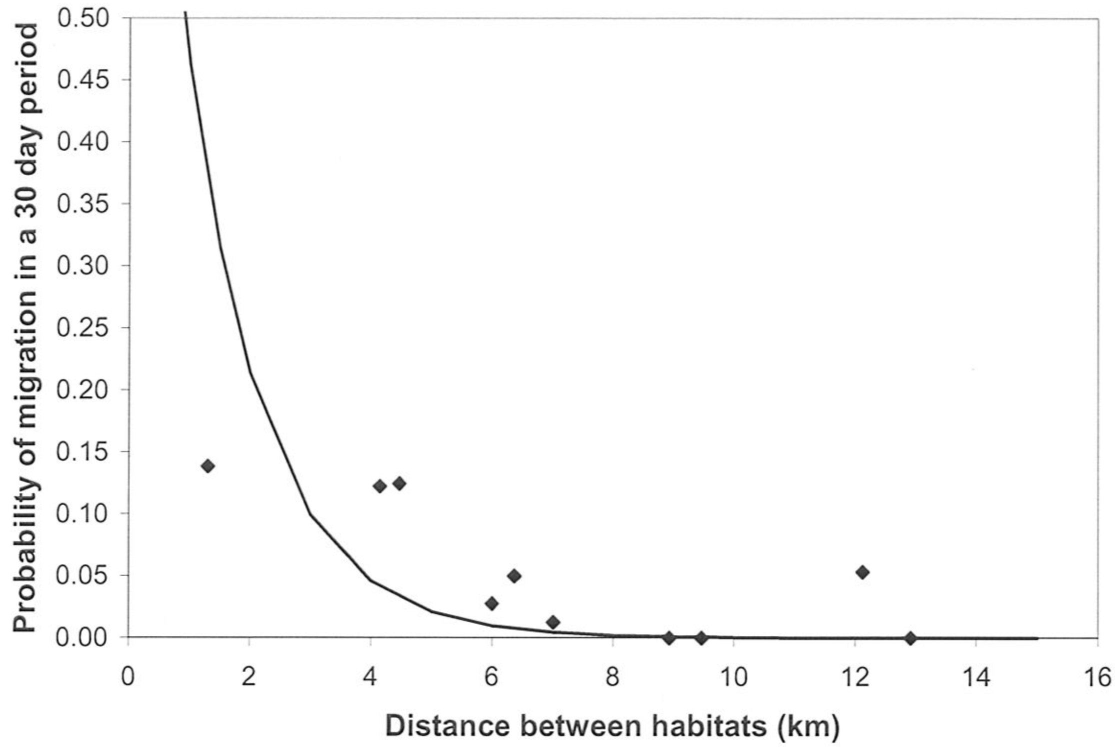

Figure 5. Relationship between distance separating two sub-populations and the probability that an adult beetle will migrate between them during a 30 day period.

had the properties that it adequately explained the capture history data with the fewest parameters. Akaike's Information Criterion (AIC) was used to identify the most parsimonious model (see Burnham and Andersen (1998) for a complete discussion of model selection theory). Once the most parsimonious model was identified, it was used to estimate daily movement probability between each sub-population pair involved in the 1994 study.

Because the metapopulation model uses a time step of one cohort, not one day, the binomial distribution was used (binomial parameter p set equal to daily movement rate) to estimate the probability that an adult beetle would migrate between two locations once within a 30 day period. It was judged that this was the approximate time period during which an individual is an active disperser, and that if a beetle dispersed within this period, it could successfully colonize and breed in the new location.

Estimates of 30-day movement probability were used to determine a best fit line for Equation 2 (i.e., to estimate the value of b). The best fit line was obtained with $b = 1.30$ (Figure 5). It should be noted that it is not strictly correct to regress movement probability on distance because the movement probability estimates from Program MARK are not independent. However, for the purpose of getting a rough estimate of the relationship between distance and dispersal, this approach was judged adequate. Equation 2 was incorporated into the metapopulation model and used to predict the probability that a beetle would migrate from one location to another, based on the distance between the locations. The net result was that populations close together (<6 km apart) tended to exchange individuals, decreasing the risk of extinction by allowing extant sub-populations to "rescue" nearby extinct ones.

Predicting Probability of Extinction Under Various Management Strategies

Program RAMAS Metapop (Applied Biomathematics, Inc., Setauket, New York) was used to model metapopulation dynamics and predict extinction probability over three planning horizons: 100 cohorts (200 years), 25 cohorts (50 years), and 5 cohorts (10 years). At the beginning of a given horizon, the starting size for each sub-population was specified (Table 1). Population abundance one cohort later was predicted based on the model-generated λ for each sub-population (generated from a normal distribution with mean λ [=1.3] and the specified standard deviation [=0.55] and accounting for correlation among sub-populations based on the distance between them); the amount of dispersal among sub-populations (also based on distance); and the specified carrying capacity for each sub-population (Table 1). This produced a predicted abundance in each sub-population at the beginning of the next cohort. The process was repeated for the desired number of cohorts (100, 25, or 5), producing a time series of abundance for that planning horizon. When a simulation was complete, original parameter values were reset to the specified initial conditions, and the model rerun. Predictions from each individual run, even if started from the same initial conditions, produced different abundance time series because of the environmental stochasticity incorporated in to the model. In order to predict extinction probability under a specified set of initial conditions, 1000 replicate model runs were made for each planning horizon. The percentage of runs that produced an extinction sometime during each planning horizon (population size reaching 0 as some point during the planning horizon) was the predicted probability of extinction for Puritan tiger beetles over that horizon.

In order to evaluate the potential effectiveness of different management strategy, seven strategies were developed based on the judgement of the second author in consultation with the Maryland Department of Natural Resources (Table 5). Each strategy represented a different set of sub-populations being protected from shoreline alteration. The metapopulation model was adjusted for each strategy to include only the sub-populations that would be protected under that strategy

Table 5. Management strategies developed for Puritan tiger beetles in the Chesapeake Bay region. Each strategy was evaluated based on predicted extinction risk as determined by a metapopulation model. PMS=Parker Marsh South, CCSP=Calvert Cliffs State Park, CCNP=Calvert Cliffs Nuclear Plant, SC=Scientists Cliffs, WS=Western Shore/Calvert Beach, CC=Cliffs of Calvert, R=Randle, LCP=Little Cove Point, BF=Bayside Forest, SNRMA=Sassafras NRMA, GP=Grove Point, OP=Ordinary Point, ET=East Turner, EL=East Lloyd Creek, EB=East Betterton, WB=West Betterton, NS= North Still Pond.

Strategy	Calvert County	Sassafras River
1	All sites	All sites
2	PMS, CCSP, CCNP, SC, WS	SNRMA, GP, NS, WB, EL, OP
3	PMS, CCSP, WS, CCNP, LCP	SNRMA, GP, NS, WB, EB, ET
4	PMS, CCSP, BF, WS, CCNP, LCP, CC	SNRMA, GP, NS, OP, EB, ET
5	PMS, CCSP, R, BF, WS, CCNP	SNRMA, NS, WB, OP, EL, EB
6	PMS, CCSP, SC, R, CCNP, CC	SNRMA, NS, WB, EL, EB, ET
7	PMS, CCSP	SNRMA, GP, NS, WB
8	PMS, CCSP, CCNP, SC, WS, CB, R	SNRMA

(i.e., all other sub-populations were assumed to be lost to shoreline alteration or other habitat impacts). The goal was to determine which strategy produced the lowest extinction probability. To provide a baseline for comparison, a default strategy was used that included all sub-populations known to be extant in 2004. Modeling was completed for the Calvert County and Sassafras River metapopulations individually, and for each sub-population independently of the others (i.e., as a single population that is not part of a metapopulation).

Effect of Habitat Improvement on Extinction Risk

In addition to protection of certain combinations of sub-populations, management can include habitat improvement with the goal of increasing carry capacity at a given site. Such improvements would most likely occur at sites already under local, state, or Federal protection, which include Parker Marsh South in Calvert County and Sassafras NRMA in Sassafras River. To evaluate the efficacy of habitat improvement, we altered the metapopulation model to include increased carrying capacity at these two sites. The original model used K=618 for Parker Marsh South, and we increased this to 1,500 for the habitat improvement model. For Sassafras NRMA the original model used K=19 and the habitat improvement model used K=200. To evaluate the potential benefits of habitat improvement, we compared extinction probabilities from the new model to those predicted by the original metapopulation model.

Sensitivity Analysis

Because important parameters in the model were only roughly estimated, a sensitivity analysis was conducted to evaluate if using different parameter values changed conclusions regarding which management strategies were best. The metapopulation was adjusted to include a higher level of annual stochasticity in population growth rate (standard deviation of annual growth rate = 0.8 rather than 0.55), no dispersal, or no correlation in growth rate among populations. All management strategies in each metapopulation were re-run under each condition. The relative effectiveness of each management strategy was compared for both models in order to determine if alternative parameter values in the model changed conclusions about which strategy is optimum.

Results and Discussion

Model Results

Results from the metapopulation model indicate that the probability of extinction within each metapopulation over the next 100 cohorts is high if no additional sites are protected beyond those already included under state, federal, or private plans to preserve beach habitat (Table 6, Strategy 7 for Calvert County and 8 for Sassafras River). The two protected sites in Calvert County are Calvert Cliffs State Park and Parker Marsh South. If only these sites remain protected (and the other populations lost to habitat alteration), the metapopulation model predicts a 94% chance that the metapopulation will go extinct within the next 100 cohorts, a 55% chance of extinction in the next 25 cohorts, and a 17% chance in the next 5. The only protected site in the Sassafras River metapopulation is the Sassafras NRMA. If it is the only site protected, the model predicts that extinction is essentially certain within 100 cohorts (probability >99.99%), almost certain within 25 cohorts (84% probability), and not unlikely over the next 5 (24% probability).

Table 6. Summary of extinction probability results from a metapopulation model of Puritan tiger beetles in the Chesapeake Bay region. The probability that the population will fall below 0 or 500 animals sometime during the next 100, 25, and 5 cohorts is shown for the Calvert County and Sassafras River metapopulations. Probabilities were developed under each of eight management strategies (Table 5).

	Probability of the metapopulation falling to 0 or to 500 animals sometime during the next:											
	100 Cohorts				25 Cohorts				5 Cohorts			
	Calvert County		Sassafras River		Calvert County		Sassafras River		Calvert County		Sassafras River	
Strategy	0	500	0	500	0	500	0	500	0	500	0	500
1 (all sites)	0.00	0.82	0.07	1.00	0.00	0.30	0.01	1.00	0.00	0.02	0.00	0.56
2	0.05	0.98	0.10	1.00	0.01	0.56	0.02	0.99	0.00	0.07	0.00	0.59
3	0.04	0.96	0.17	1.00	0.00	0.54	0.03	1.00	0.00	0.09	0.01	0.69
4	0.01	0.94	0.28	1.00	0.00	0.46	0.05	1.00	0.00	0.06	0.00	0.74
5	0.04	0.99	0.18	1.00	0.00	0.58	0.03	1.00	0.00	0.08	0.00	0.89
6	0.20	1.00	0.22	1.00	0.01	0.70	0.05	1.00	0.00	0.12	0.01	0.93
7	0.94	1.00	0.24	1.00	0.55	1.00	0.07	1.00	0.17	0.86	0.01	0.77
8	0.03	0.96	1.00	1.00	0.01	0.50	0.84	1.00	0.00	0.05	0.24	1.00

Conversely, if all currently extant sub-populations could be protected, predicted extinction probability is low for both metapopulations (Table 6, Strategy 1; extinction probability 0% for Calvert County and 7% for Sassafras River over the next 100 cohorts). However, there would still be a high probability that total abundance in each metapopulation would fall to critically-low levels sometime within the next 100 cohorts. For example, the metapopulation model predicts an 82% chance that total populations will drop below 500 at Calvert Cliffs (Table 6). The Sassafras River metapopulation will almost certainly fall below 500 individuals sometime within 100 cohorts. We believe that if the total population at each metapopulation falls below 500, the chances of extinction from catastrophic events, Allee effects, and from loss of genetic diversity (none of these effects are not included in the model) will be very high. Thus, these populations face serious risk even under the best of circumstances, and a well-designed program of beach protection is required to have any hope of avoiding extinction in the Chesapeake Bay region.

In order to compare management strategies in more detail, interval extinction risks were summarized graphically (Figure 6 for the Calvert Cliffs metapopulation and Figure 7 for the Sassafras River metapopulation). Interval extinction risk is defined as the probability that beetle abundance will drop below a specified threshold population size sometime during the next specified number of cohorts. If the threshold is set at 0, then interval extinction risk is equal to the risk of extinction. However, if thresholds above 0 are considered, then the ability of a given management strategy to maintain beetle abundance above certain critical thresholds can be examined. The easiest way to use the figures is to look for lines shifted as far to the right as possible. Those lines represent strategies that reduce extinction risk the most (notice that the "All Sites" strategy is always the right-most line). By looking at the spacing of the lines, one can judge the relative effectiveness of a given strategy. Notice also that lines shift to the right as the planning horizon is shortened (100 versus 25 versus 5 cohorts) because there is a lower probability that the metapopulation will go extinct over the next 5 cohorts as compared to the next 100.

At the Calvert Cliffs metapopulation, Strategy 4 provides the best overall protection short of protecting all sites (Figure 6). This strategy calls for protection of 7 sub-populations (Table 5), and the effectiveness is related to the fact that the sites are spaced all along the coastline, allowing for relatively easy dispersal among sites. The potential for dispersal among sites seems to be the critical issue in maintaining the metapopulation (this issue will be examined in more below), and strategies which feature protection of a contiguous line of adjacent sites seem to work better than those in which protected sites are more isolated. For example, Strategy 6 calls for protection of six sites (Table 5), but because the sites are widely-spaced, the risk is high that populations will fall to low levels.

The metapopulation model predicts that the Sassafras River metapopulation is at serious risk even if all sub-populations could be protected (Figure 7). Over the next 100 cohorts the population is predicted to almost certainly fall below 200 individuals. So, the potential to save the beetle at the Sassafras site seems limited over the long-term. However, some strategies are better than others when a shorter planning horizon is considered. For example, Strategy 7, which includes protection of only four sites (Table 5) affords almost as much protection over the next 5 cohorts as does protection of all 8 sites. Similarly, if the next 25 cohorts are considered, Strategy 2 (which includes protection of 6 sites) affords about as much protection as protecting all 8 sites.

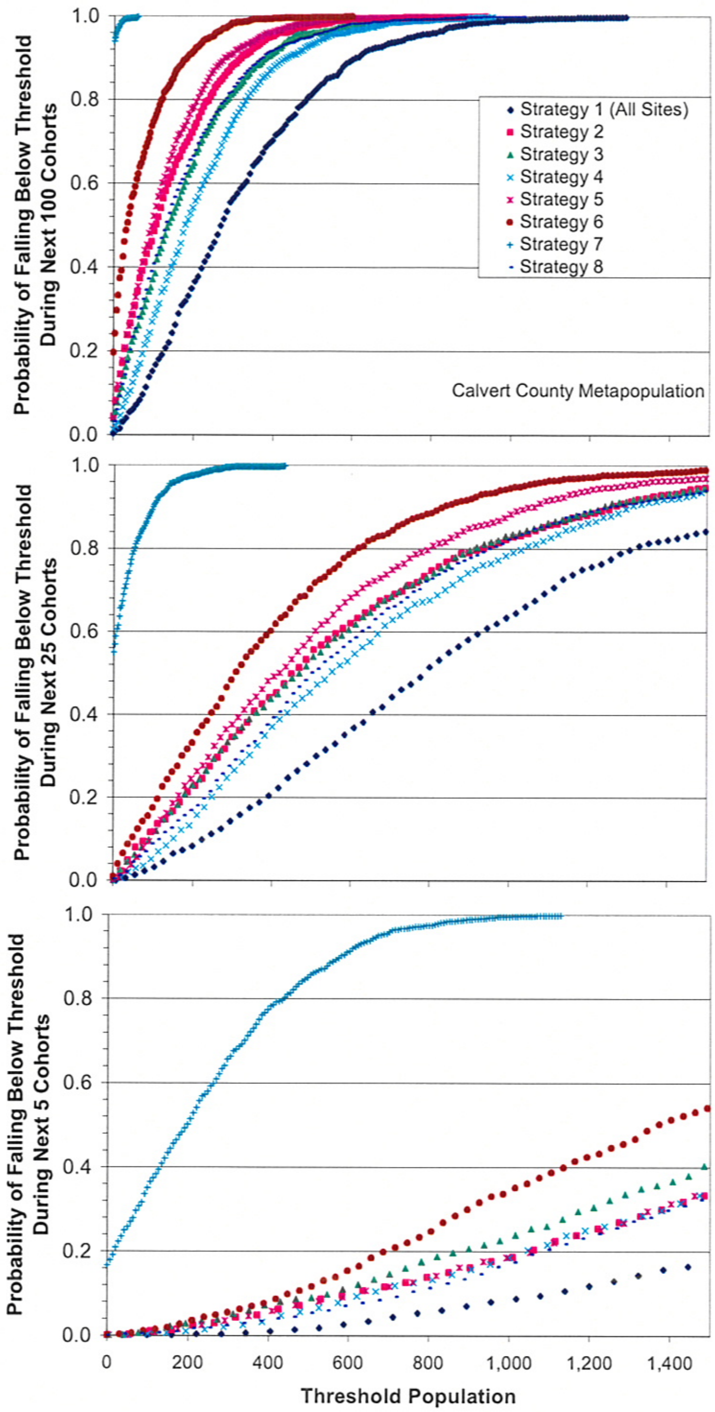

Figure 6. Interval extinction risks for Puritan tiger beetles in the Calvert County metapopulation in the Chesapeake Bay region. Risks are shown for a period of 100 cohorts (upper panel), 25 cohorts (middle panel) and 5 cohorts (lower panel).

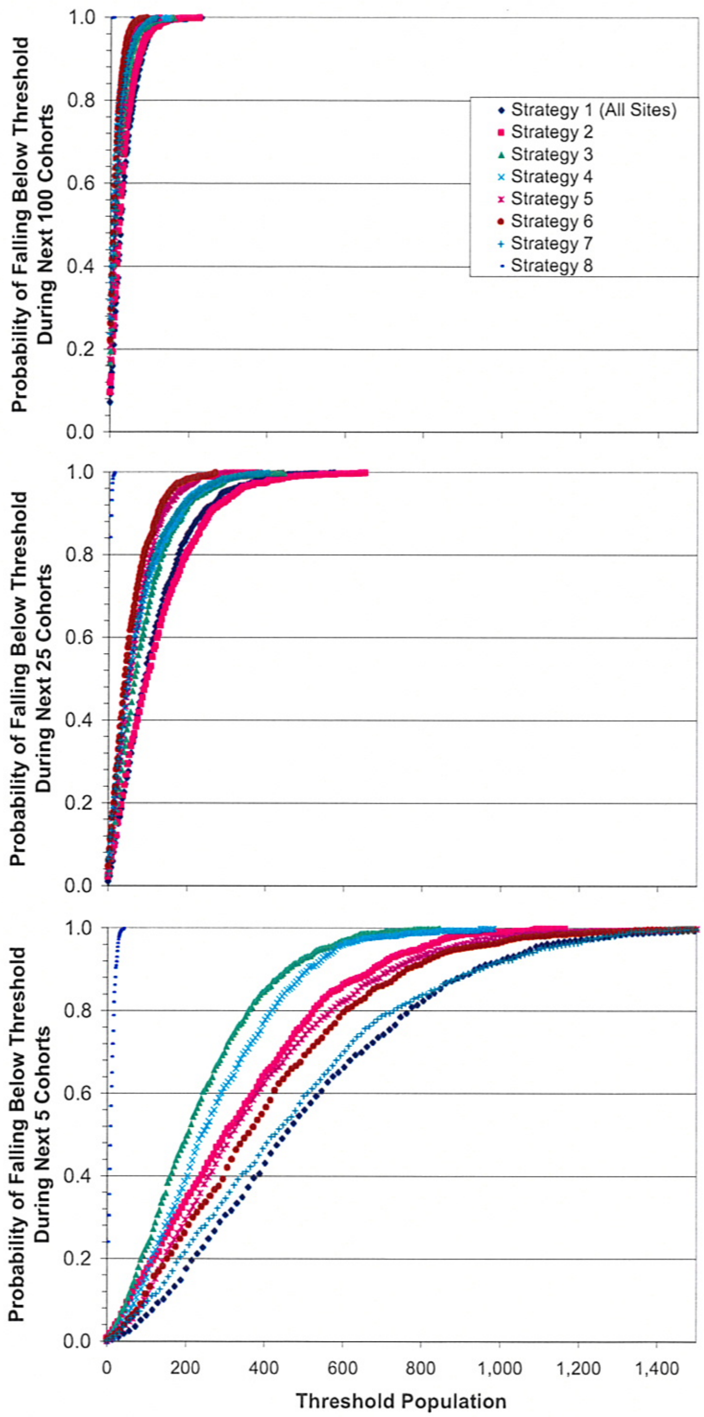

Figure 7. Interval extinction risks for Puritan tiger beetles in the Sassafras River metapopulation in the Chesapeake Bay region. Risks are shown for a period of 100 cohorts (upper panel), 25 cohorts (middle panel) and 5 cohorts (lower panel).

In order to examine worst-case scenarios, we modeled extinction probability for each sub-population individually (i.e., a site was modeled as if it were the only extant population). Under these circumstances, the model predicted that individual sub-populations cannot be self-sustaining, even those with relatively large carrying capacities such as Calvert Cliffs State Park (Figure 8). This indicates that persistence of the species requires multiple sub-populations linked in a metapopulation, and that dispersal (i.e., recolonization of vacant habitat) is the critical mechanism by which the species maintains itself over time. Thus, the loss of each additional sub-population increases risk of extinction. More insight into this issue is provided under "*Sensitivity Analysis*", below)

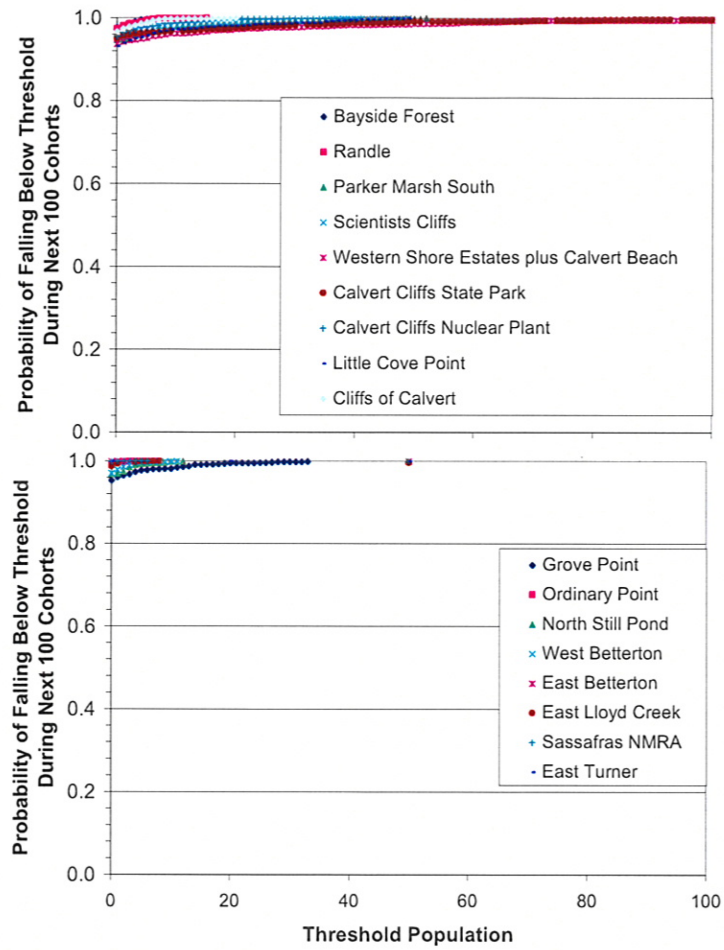

Figure 8. Interval extinction risks for Puritan tiger beetles in the Calvert Count (upper panel) and Sassafras River (lover panel) metapopulations in the Chesapeake Bay region. Risks are for each individual sub-population treated as if it were the only sub-population in existence.

Effect of Habitat Improvement on Extinction Risk

In order to evaluate the potential effectiveness of habitat improvement at specific sites, carrying capacity at Parker Marsh South and Sassafras NRMA was increased and the effects on extinction probabilities evaluated. The evaluation focused on those management strategies that were most effective (Strategies 1, 4 and 8 at Calvert County and 1, 2, and 3 at Sassafras River). Results indicate that increasing carrying capacity can reduce extinction risks at both Calvert County and Sassafras River (Figure 9), although the effects are relatively small. For example, habitat enhancement would lower the probability that the Calvert County population falls below 500 individuals from an estimated 82% without habitat enhancement to about 75% with enhancement. Similar effects are seen at Sassafras River. Still, given the generally-high risk of extinction these beetles face, even minor reductions in risk may be important.

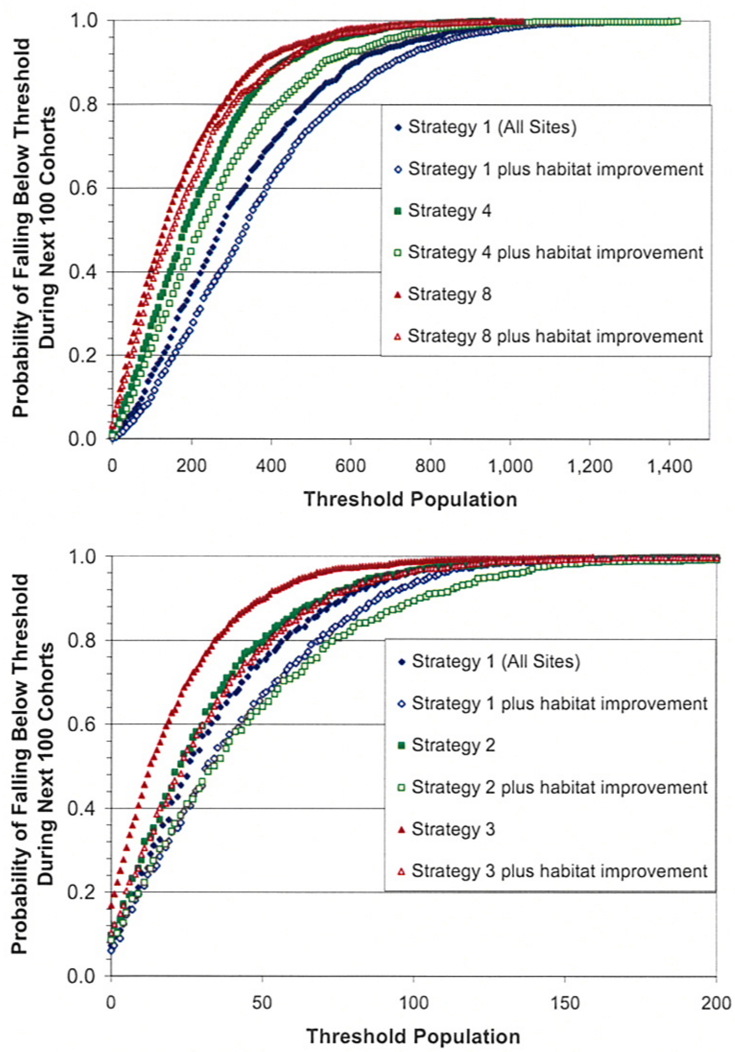

Figure 9. Interval extinction risks over 100 cohorts for Puritan tiger beetles in the Calvert Count (upper panel) and Sassafras River (lover panel) metapopulations in the Chesapeake Bay region. Risks were predicted using two models, including one with existing carrying capacities at each sub-population, and one with increased carrying capacities at certain sites due to habitat improvement. Models were run under a variety of management strategies involving the protection of specific sub-populations (see Table 5). Notice that the x-axis scale is different in the two panels because extinction probabilities are much higher at the Sassafrass River metapopulation.

Sensitivity Analysis

Because most model parameters could only be roughly estimated, a sensitivity analysis was used to evaluate the effect that alternative parameter values have on predicted extinction probability. To evaluate this, we ran three alternative models: one with no dispersal, one with no correlation in growth rates, and one with high stochasticity in growth rates. The initial analysis included all extant sub-populations (Strategy 1) over a planning horizon of 100 cohorts. Results from both the Calvert County and Sassafras River metapopulations indicated that making different assumptions about dispersal, correlation, and stochasticity significantly influenced predicted interval extinction risks (Figure 10). Compared to the default model (i.e., the one that uses our best estimates for each parameter value), models without dispersal and with high stochasticity predicted significantly higher extinction risks. Conversely, models with no correlation predicted much lower extinction risks than the default model.

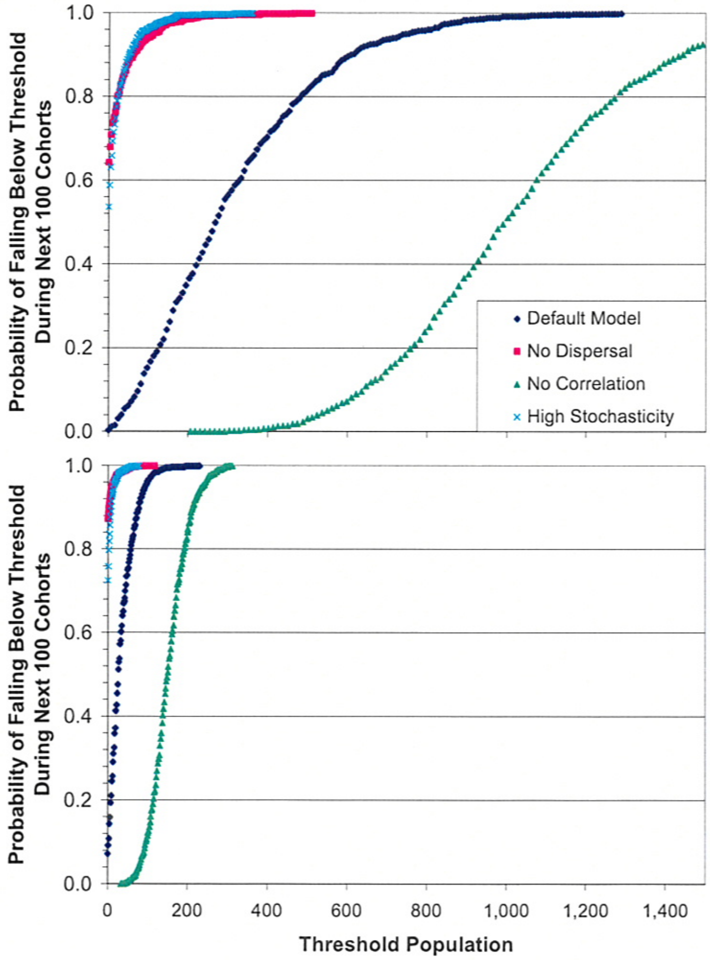

Figure 10. Interval extinction risks over 100 cohorts for Puritan tiger beetles in the Calvert Count (upper panel) and Sassafras River (lover panel) metapopulations in the Chesapeake Bay region. Risks were predicted using four models, including one with best-estimates for each parameter ("default model"), one with no dispersal among sub-populations, one with no correlation in growth rates among sub-populations, and one with high stochasticity (variation) in cohort growth rates.

That different parameter values influence predicted extinction risks is not surprising and reinforces the fact that predicted risks presented in this report should not be taken as literally true. Instead, the main intent is to identify management strategies that work better than others to reduce extinction risk, regardless of the exact numerical value of the predicted risk. Therefore, what is most important is to identify those strategies which consistently rank as the best regardless of which particular parameter values are used. The ideal strategy would be one that worked well under a wide-range of model parameters, meaning that even if we were wrong about certain parameter values, we could still correctly identify which management strategies worked best. To examine this issue, we compared predicted extinction probabilities for each strategy under each alternative model. For each model, we ranked strategies from 1 (lowest risk of extinction) to 8 (highest risk of extinction) and compared average rankings across models (Table 7). As expected, the strategy that includes protection of all sub-populations (Strategy 1) ranks as best (rank =1) under all models. In the Calvert County metapopulation, Strategies 4 and 8 (each with an average rank of 2.9) worked consistently well under all models. In the Sassafras River metapopulation, Strategy 2 (average rank = 2.8) is the only strategy that worked consistently well under all models.

Table 7. Extinction-probability predictions for each of eight management strategies (see Table 5) using four metapopulation models. The Default Model includes best estimates for parameters related to dispersal, correlation in growth rates, and stochasticity in growth rates. The No Dispersal model assumes that there is no dispersal among sub-populations. The No Correlation model assumes that there is no correlation in cohort growth rates among sub-populations. The High Stochasticity model includes uses 0.8 as the standard deviation of cohort growth rates (default model=0.55). Simulations were made for two metapopulations existing in Chesapeake Bay. The overall best strategy for a metapopulation is the one with the lowest Average Rank because it performs well regardless of which model parameters are used.

	Default Model		No Dispersal		No correlation		High Stochasticity		
Strategy	Extinction Probability	Strategy Rank	Extinction Probability	Strategy Rank	Extinction Probability	Strategy Rank	Extinction Probability	Strategy Rank	Average Rank
Calvert County Metapopulation									
1	0.00	1	0.64	1	0.000	3.5	0.54	1	1.6
2	0.05	6	0.78	3	0.000	3.5	0.74	4	4.1
3	0.04	4	0.82	7	0.000	3.5	0.76	5	4.9
4	0.01	2	0.79	4	0.000	3.5	0.65	2	2.9
5	0.04	5	0.80	6	0.000	3.5	0.83	6	5.1
6	0.20	7	0.79	4	0.003	7	0.96	7	6.3
7	0.94	8	0.94	8	0.948	8	1.00	8	8.0
8	0.03	3	0.75	2	0.000	3.5	0.73	3	2.9
Sassafras River Metapopulation									
1	0.073	1	0.873	1	0.000	1	0.73	1	1.0
2	0.097	2	0.888	2.5	0.001	4	0.81	2	2.6
3	0.169	3	0.888	2.5	0.001	4	0.89	4	3.4
4	0.280	7	0.902	4	0.001	4	0.93	6	5.3
5	0.176	4	0.912	5	0.001	4	0.87	3	4.0
6	0.223	5	0.927	7	0.001	4	0.90	5	5.3
7	0.238	6	0.914	6	0.026	7	0.95	7	6.5
8	0.999	8	0.999	8	0.999	8	1.00	8	8.0

Summary and Recommendations

Strategies that include only protected sites (Strategy 7 in Calvert County, which includes protection of Parker Marsh South and Calvert Cliffs State Park, and Strategy 8 at the Sassafras River which includes protection of just the Sassafras NRMA) provide almost no protection from extinction. It is vital that sites beyond those currently protected be included in future management strategies. In Calvert County, the overall best strategies of those examined are Strategy 4 (protection of Parker Marsh South, Calvert Cliffs State Park, Bayside Forest, Western Shores/Calvert Beach, Calvert Cliffs Nuclear Plant, Little Cove Point, and Cliffs of Calvert) and Strategy 8 (protection of Parker Marsh South, Calvert Cliffs State Park, Calvert Cliffs Nuclear Plant, Scientists Cliffs, Western Shores/Calvert Beach, and Randle). At the Sassafras River, the overall best strategy of those examined is Strategy 2 (protection of Sassafras NRMA, Grove Point, North Stillpond, West Betterton, East Lloyd, and Ordinary Point). Habitat enhancement at Parker Marsh South and Sassafras NRMA would marginally reduce the risk of extinction, and we recommend that such enhancements be included in any final management plan.

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